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Estimated size of the Northwest Atlantic grey seal population 1977-2007

Évaluation de la population de phoques gris de l'Atlantique Nord-Ouest, 1977 – 2007

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ABSTRACT

We constructed a stochastic model of Northwest Atlantic grey seal population dynamics and fit it to available pup production data from 1977-2007 divided into three breeding regions: Sable Island, Gulf of St. Lawrence, and Eastern Shore (including Hay Island and other small colonies along coastal Nova Scotia). The model assumes that fecundity rates are age-dependent but are constant over time, that adult survival rates are constant, and that pup survival is density dependent. Females are assumed to be able to move to a new region to breed if pup survival is higher there, but once they start breeding they do not move. We used a Bayesian computer-intensive method (particle filtering) to fit the model, with informative priors on model parameters. The posterior estimates for some parameters were close to their priors, indicating little information about these parameters in the pup production data and highlighting the importance of carefully choosing the priors. Other parameters were far from the prior: in particular the posterior estimates of carrying capacity were far higher than the prior values, indicating little evidence of density dependent population regulation at current levels of pup production. The total estimated population size at the end of the 2007 breeding season (i.e., including pups) was 304,000 (95% CI 242,000-371,000). This is 6% higher than the equivalent estimate for 2006 of 285,000 (95%CI 230,000-344,000) and 750% higher than the estimate for 1977 of 41,000 (95%CI 31,000-51,000). Average annual rates of population increase are estimated to be 4% in the 1980s (lower due to greater harvests in the Gulf), 9% in the 1990s and 8% in the 2000s. These estimates should be treated with some caution because: (1) the biological model showed clear lack of fit, particularly to the Gulf data where extending the model to account for ice and weather conditions would be useful; (2) sensitivity of the results to the priors used has not been assessed; and (3) the fitting algorithm may have caused some biases.

RESUMÉ

Nous avons élaboré un modèle stochastique de la dynamique de la population de phoques gris de l'Atlantique Nord-Ouest et y avons intégré les données existantes de production des jeunes phoques de 1977 à 2007, issues de trois aires de reproduction : l'île de Sable, le golfe du Saint-Laurent et la côte est (y compris la colonie de l'île Hay et d'autres petites colonies situées le long de la plateforme Néo-Écossaise). Le modèle permet de supposer que les taux de fécondité dépendent de l'âge, mais qu'ils demeurent néanmoins constants dans le temps, que les chances de survie des petits phoques sont liées à la densité, que les femelles sont capables de se déplacer vers une autre région pour se reproduire si les chances de survie des bébés phoques y sont plus élevées, mais qu'une fois fécondées, elles ne bougent plus. Nous avons employé une méthode bayésienne reposant largement sur le traitement informatique (filtrage de particules) pour l'adaptation d'information a priori sur les paramètres du modèle. Les estimations postérieures de certains paramètres se sont montrées relativement proches des données a priori, révélant l'existence de très peu d'information sur ces paramètres dans les données sur la production des bébés phoques et faisant ressortir l'importance de bien choisir les éléments a priori. Par contre, d'autres paramètres étaient très éloignés de l'information a priori, surtout dans le cas des évaluations postérieures de la capacité de charge, qui étaient beaucoup plus élevées que les valeurs a priori, montrant très peu de signes d'une dépendance de la régulation de la population à l'égard de la densité, au taux actuel de production des petits. En 2007, l'estimation de la population (comprenant les petits) au terme de la saison de reproduction était de 304 000 (IC de 95 % = 242 000 – 371 000). Cela représente une hausse de 6 % par rapport à l'estimation comparable de 2006 qui totalisait 285 000 (IC de 95 % = 230 000 – 344 000) et de 750 % comparativement à celle de 1977 qui était de 41 000 (IC de 95 % = 31 000 – 51 000). Au cours des années 1980, la progression annuelle de la population était évaluée à 4 % (en raison des captures plus nombreuses dans le Golfe), à 9 % durant les années 1990 et à 8 % pendant les années 2000. Il importe toutefois d'user de prudence dans la mention de ces estimations puisque : 1) le modèle biologique a révélé une très faible corrélation, surtout en ce qui concerne les données du Golfe où il serait utile d'élargir la capacité du modèle de manière à tenir compte de l'état des glaces et des conditions météorologiques, 2) la sensibilité des résultats aux valeurs a priori n'a pas été évaluée et 3) l'algorithme employé est susceptible d'avoir introduit certaines erreurs.

INTRODUCTION

The aim of this paper is to present preliminary estimates of population size for the Northwest Atlantic grey seal (*Halichoerus grypus*). Seals (and marine mammals in general) are notoriously difficult to census: they spend much of their time at sea and most of that underwater. The only time a substantial part of the population is in one place is during the breeding season, when pre-weaned pups are readily counted on breeding colonies, and for this reason pup production estimates form the principal tool for population monitoring.

The breeding population of Northwest Atlantic grey seals is normally divided into two components for management purposes, based on the locations of the largest breeding colonies. These are the Sable Island component and traditionally a Gulf of St. Lawrence (Gulf) component (Mansfield and Beck 1977). However, recent changes in the distribution of pupping warrant dividing the population into three parts, for the purposes of modelling, which we refer to as "regions": Sable Island, Gulf and Eastern Shore (Fig. 1). Pup production on Sable Island has been relatively well monitored, with pup production estimated in most years from 1962 to 1990 by tagging all weaned pups (Mansfield and Beck 1977, Stobo and Zwanenburg 1990) and more recently at longer intervals via aerial photography (Bowen et al. 2007). The Gulf region comprises animals that whelp primarily on the drifting pack ice in Northumberland Strait and those born on small islands located within the southern Gulf of St. Lawrence. Pup production here has been estimated approximately every 4 years from mark-recapture studies (Hammill et al. 1992, 1998, Myers et al. 1997) and aerial surveys (Hammill and Gosselin 2005; Hammill et al. 2007). The estimates have higher standard errors (SEs) than those from Sable Island because of more difficult conditions in this area (Myers et al. 1997, Hammill et al. 1998). The third region, the Eastern shore, is by far the smallest part of the population. It comprises seals that whelp primarily on Hay Island, but also includes some other small islands along the eastern shore of Nova Scotia. These have been monitored intermittently by visual counts or year-class tagging (Hammill et al. 2007). All three regions were surveyed most recently in spring 2007 (Hammill et al. this meeting). The pup production data used here are shown in Appendix Table A1.

To estimate total population size from pup production data, it is necessary to make assumptions about the relationship between pup production and numbers of seals in other age classes, and between observed and actual pup production. We do this using a stochastic discrete-time modelling framework called a state-space model. The use of this framework to describe and fit models of wildlife population dynamics is described by Buckland et al. (2004), and examples of its application to the British population of grey seals are given by Thomas et al. (2005), Newman et al. (2006) and Buckland et al. (2007). Similar models to those employed here have been used to provide advice on British grey seals population size to the UK Special Committee on Seals since 2003 (Thomas and Harwood 2003, 2004a, b, 2005, 2006, 2007).

We follow the most recent population analysis of Northwest Atlantic grey seal pup production data (Trzcinksi et al. 2006) in considering population dynamics models that allow for density dependent declines in vital rates in response to increases in population size. We initially considered as feasible that there is either density dependent decline in age-specific fecundity or pup survival.

Specifying complex models for wildlife population dynamics is relatively simple, but fitting them to observed data is often not so straightforward (Buckland et al. 2007, Newman et al. in revision). We employ a computer-intensive Bayesian fitting method called Monte Carlo particle filtering (also called sequential importance sampling). A particle filter is an algorithm that produces a set of weighted samples (particles) taken from the prior distributions on the parameters and states (seal numbers) and projected forward stochastically through the time series. The weights relate to the manner in which the particles were sampled, how they were projected forward and the likelihood of the observed pup production given the simulated pup numbers. An accessible tutorial in the context of state-space models for wildlife population dynamics is given by Newman et al. (2006), and applications using particle filters are given by Thomas et al. (2005) and Thomas and Harwood (2003, 2004a, b, 2005, 2006, 2007). A general comparison between particle filtering and other fitting methods, such as Markov chain Monte Carlo (MCMC) in this context is given by Buckland et al. (2007), and a detailed comparison using a state-space model for British Grey seals applied to real and simulated data is given by Newman et al. (in revision).

Bayesian methods require prior distributions to be specified for all random quantities. We use informative prior distributions on model parameters, such as survival rates, fecundity rates and movement parameters. These are mostly taken from expert opinion, but our prior on fecundity rates comes from an analysis of pregnancy rates as a function of age in a sample of females taken as part of a scientific sampling program between 1969 and 2007. This analysis is also informative about suitable choice of biological model, in that it is possible to examine whether pregnancy rate has changed over time, possibly as a result of density dependence.

MATERIALS AND METHODS

Analysis of pregnancy rate data

Samples of females were shot between 1969 and 2007 and examined for pregnancy status and age. Pregnancy rates are known to vary with age, and are thought to have declined in recent years, particularly in immature females (around age 4) (Hammill and Gosselin, this meeting). We examined this, using the above data, initially graphically and then using generalized additive modelling (GAM), with the response variable (pregnancy status) being binomial and potential covariates age and year (as either factors or smooth functions). These analyses were performed using the mgcv package in R version 2.5.1 (R Development Core Team 2007).

Smooths produced by GAM do not make ideal prior distributions as they are not simply expressed in terms of a low-dimensional parametric function. Therefore, to provide priors distributions for age-specific fecundity rates for the state-space model fitting, we searched for a low-dimension curve that was a good approximation to the above analysis results, using nonlinear least squares to fit suitable candidate models (function nls in R 2.5.1). The dependent variable in this analysis was observed proportion pregnant, and each observation of the proportion pregnant was weighted by the square root of sample size.

State-space model

A state-space model has two components: (1) the state process, which models the true but unknown state of the population (in this case numbers of seals of different ages in different regions); and (2) the observation process, which models how the survey data are generated given the true states.

Our findings from the analysis of pregnancy rate data (see *Results*, below) guided many of our choices in constructing the state process. We divided the seal population in each breeding region into 7 age classes: pups (age 0), age 1 to 5 adult females, and age 6 and older females. Note that our model does not explicitly include adult males – see below for assumptions required to calculate male population numbers.

The time step for the process model is 1 year, beginning just after the breeding season. The model is made up of 5 sub-processes: harvest, survival, ageing, movement of age 3 females, and breeding.

Harvest consists of removal of what are assumed to be known numbers of animals, killed as a result of the commercial hunt as well as scientific sampling. The annual harvest data were divided into pups, "juveniles" (assumed to be age 1-3) and "adults" (age 4+). Within these latter two groups, the numbers of each age removed from the population were assumed to be in proportion to their relative frequency in the population. For example, if 72 juveniles were known to have been removed in a particular year, and there were estimated to be 100, 80 and 60 seals of age 1, 2 and 3 respectively, then we assumed that 30, 24 and 18 animals were removed from each age class, respectively.

Survival is modelled as a binomial random process, and is assumed additive to harvest (i.e., occurring after numbers removed by harvest). We assume that pup survival is density dependent, and follows a Beverton-Holt function of the form:

$$\phi_{p,r,t} = \frac{\phi_{p\max}}{1+\beta_r n_{0,r,t-1}} \qquad (1)$$

where $n_{0,r,t-1}$ is the number of pups born in region r in year t-1, $\phi_{p,r,t}$ is survival rate of these pups, $\phi_{p\max}$ is maximum pup survival rate, and β_r is inversely proportional to the carrying capacity of the region ($\beta \geq 0$). We assume that half of the pups born will be male; hence the expected number of female pups surviving will be $0.5\phi_{p,r,t}n_{0,r,t-1}$. We assume that adult female survival rate, ϕ_a is constant across regions and time.

Ageing is deterministic – all seals age by one year (although those in the age 6+ category remain there).

To model movement, we assume that only females age 3 (i.e., before breeding age) may move from their natal region, and thereafter females remain in the region they are in. We assume that movement is fitness dependent, such that females will only move if the expected survival of their future offspring is higher elsewhere, and the probability of movement is proportional to the expected survival difference. We measure the propensity for fitness-dependent movement relative to a competing propensity for site fidelity, which means that many females will not move even if conditions for their pups

would be better elsewhere. We assume that numbers in each region after movement is a multinomial random variable:

$$\left(n_{2,1,t}, n_{2,2,t}, n_{2,3,t}\right) \sim Multinomial\left(\sum_{r=1}^{3} n^{*}_{2,r,t}, p_{1,t}, p_{2,t}, p_{3,t}\right) \qquad (2)$$

where $n^{*}_{2,r,t}$ and $n_{2,r,t}$ denote numbers of age 2 females in region r before and after movement respectively, and $p_{r,t}$ is the probability that a seal aged 2 is in region r after movement. We model this probability as

$$p_{r,t} = \frac{\sum_{j=1}^{3} n^{*}_{2,j,t} \delta_{j \to r,t}}{\sum_{j=1}^{3} n^{*}_{2,j,t}} \qquad (3)$$

where

$$\delta_{j \to r,t} = \frac{I[j = r] + \gamma \max\left(\phi_{p,r,t} - \phi_{p,j,t}, 0\right) I[j \neq r]}{1 + \gamma \max\left(\phi_{p,r,t} - \phi_{p,j,t}, 0\right)} \qquad (4)$$

with $I[.]$ being an indicator function that takes value 0 if the condition inside the bracket is met and zero otherwise, and γ being a parameter regulating the strength of density-dependent movement versus site fidelity (the larger γ, the stronger the effect of density dependence; $\gamma \geq 0$). This movement model is a simpler version of that used by Newman et al. (in revision), which had an additional parameter to make movement less likely among more widely spaced regions.

We model breeding by assuming that the number of pups produced is a binomial random variable. Following the analysis of pregnancy rate data reported below, we assume the rate is age dependent, but not time dependent. We assume that females age 3 or less at the time of the breeding season do not breed, while fecundity rate for females of age 6+ at the time of the breeding season is governed by a model parameter $\alpha_{\max}$. For females age 4 and 5, fecundity rates are given by

$$\alpha_a = \alpha_{\max} \text{logit}^{-1}(\rho(a - 4.5)) \qquad (5)$$

where ρ is a model parameter that determines how fecundity rate increases with age ($0 \leq \rho < 1$) towards $\alpha_{\max}$.

For the observation process, we assume that pup production estimates follow a normal distribution, with known standard error.

In summary, there are 8 model parameters: adult survival ϕ_a, maximum pup survival $\phi_{p\max}$, one carrying capacity parameter-related parameter for each region $\beta_1 - \beta_3$, a parameter regulating movement rates γ, maximum fecundity $\alpha_{\max}$, and a parameter regulating increase in fecundity with age, ρ.

Data and priors

The input data were pup production estimates for 1977-2007, together with their estimated standard errors (SEs, Appendix Table A1). To allow the fitting algorithm to produce reliable results in the time available to run it, the SEs in Table A1 were multiplied by 3 in the analyses reported here (see *Discussion*).

Both aerial survey and mark recapture based estimates were available for the Gulf region for 1984, 1985, 1986, 1989 and 1990; in these case a variance-weighted mean of the estimates and corresponding SE was calculated.

No SE estimates were available for Sable Island from 1977 to 1989 and for Eastern Shore for 1996, 1997 and 2000 because these were all complete counts. However, it is not appropriate to assume zero error both because this is likely inaccurate in fact, and also because the particle filtering algorithm used here will not work if with zero error values. Therefore, SEs were estimated by assuming that the ratio of estimate to variance of estimate was constant, and using a constant of proportionality for this relationship estimated from the Sable and Eastern Shore regions data that did have SE estimates associated with them.

Harvest data (Fig. 2 and Appendix Table A2) were segregated into pups, juvenile females (ages 1-3) and adult females (ages 4+), as described previously.

Prior parameter estimates are given in Table 1. Priors on fecundity rates come from the analysis of pregnancy rate data. Priors on other parameters came from previously published papers, supplemented by expert opinion.

We followed Thomas and Harwood (2005, 2006, 2007) in using a re-parameterization to specify the prior on the β_r s in terms of a prior on the pup production at carrying capacity, χ_r, conditional on the values of the other model parameters. For the model outlined above, it can be shown that expected pup survival rate at equilibrium, ϕ_p^* is given by

$$\phi_p^* = \frac{1}{0.5\phi_a^3\left(\alpha_4 + \phi_a\alpha_5 + \frac{\phi_a^2\alpha_{6+}}{1-\sigma_a}\right)} \qquad (6)$$

Substituting (6) into (1) and re-arranging, we find that for a given carrying capacity of pup production at equilibrium, χ_r,

$$\beta_r = \frac{1}{\chi_r}\left(\phi_{p\max}0.5\phi_a^3\left(\alpha_4 + \phi_a\alpha_5 + \frac{\phi_a^2\alpha_{6+}}{1-\sigma_a}\right) - 1\right) \qquad (7)$$

The priors on carrying capacity of pups at equilibrium were set by specifying a prior mean of approximately twice the largest observed count in each region, with a large prior variance (equivalent to CV of 50%) to reflect the uncertainty in specifying these values a priori.

The prior mean on the movement parameter was specified by calculating the value that would lead to a 10% emigration of age 3 seals from a region to one where pup survival was 0.1 higher. This value (2.5) was also given a large variance (equivalent to a CV of 100%) to reflect the arbitrary nature with which it was chosen.

Prior distributions are also required on seal population size by age and region for the first year (1977); the Markovian nature of the model means that prior distributions on population size for other years are defined automatically after specifying those in the first year and the parameters.

We based our method of specifying priors on the population size in the first year on that of Thomas et al. (2005). This method uses the first year of data to specify a prior distribution on pup numbers in each region, and then uses this distribution together with the demographic parameters to derive priors for the other age classes (see Thomas et al. 2005 for details). However, pup production estimates are not available in 1977 for the Gulf or Eastern Shore regions. For the Gulf, the only available data prior to 1977 is a relatively course aerial survey estimate of pup production in 1966 in the order of 1,500 (Mansfield 1966, Mansfield and Beck 1977). The first estimate after 1977 was 7151 in 1984 (Appendix Table A1). Assuming exponential growth between these time points yields an estimated growth rate of 9% per year and an estimate of approximately 3900 pups in 1977. This value was used as the prior mean, with a large variance (equivalent to a CV of 50%) such that an prior 95% CI on pup production in the Gulf was that it was between approximately 0 and 7800. This was achieved in practice by adding a fabricated observation to the pup production dataset: an observation of 3900 pups in 1977 with SE 1950. For the Eastern Shore region, there are no relevant data available; however our prior belief is that there were very few seals breeding there in 1977. We therefore set the pup production in that region to zero by adding a fabricated observation to the pup count dataset of zero pups in 1977 along the Eastern Shore, with zero SE.

Fitting method

The particle filtering algorithm we used is similar to that described by Thomas and Harwood (2007) and Newman et al. (2007), implemented in the C programming language. An outline of the main features of the algorithm is given below, for completeness – it is not necessary to read the rest of this sub-section to understand the results that follow. For reference, we highlight any differences from the Thomas and Harwood (2007) algorithm.

Initial rejection control. The aim of this procedure is to weed out at an early stage sets of parameter and state combinations that are simulated from the prior but clearly have very low density in the posterior, so that computer time can be focussed on areas of parameter and state space that have higher posterior density. We simulated sets of 1,000,000 particles from the prior distributions, projected them forwards from 1977 to 1978 and calculated likelihood weights based on the 1978 data. We then applied rejection control, an algorithm that probabilistically removes particles with low weight (Liu 2001), using the mean of the particles weights as the rejection control criterion. This typically resulted in about a quarter of the particles being retained. We repeated this process until we had at least 1,000,000 particles surviving the initial rejection control stage.

Auxiliary particle filter (Liu and West 2001). With this procedure, we projected forward one time step at a time, starting in 1978, initially deterministically. We then resampled the particles using the deterministic weights – i.e., according to the expected pup production in the next time period – thereby producing a set of "promising" particles. Because data for the Gulf and Eastern Shore regions were missing in many years, it seemed prudent not to follow the usual convention of resampling with probability proportional to the weights. Instead, we used the more conservative strategy (Liu 2001) of resampling with probability proportional to the square root of the weights (this is one point of difference from the Thomas and Harwood (2007) algorithm). Resampled copies of the same ancestor particle will have the same parameter values, so to maintain parameter diversity we used kernel smoothing to jitter the parameter values (see Liu and West 2001 for details). This can cause bias (Newman et al. in revision), so we kept the amount of kernel smoothing to a minimum, using a discount value of 0.9997 (a value of 1.0 results in no jittering at all; a value of 0.997 was used by Thomas and Harwood (2007)). After kernel smoothing, particles were then projected forward stochastically to the next time period, and weights were adjusted to take account of the initial resampling. The auxiliary particle filter was not used in years where there was no data in any region – in this case particles simply projected forward stochastically, without any re-weighting or resampling.

Final rejection control. At the last time period, rejection control was used to reduce the number of particles that must be stored. The rejection control criterion was the mean of the particle weights. This reduced the number of particles stored per run from 1,000,000 to between 600,000 and 700,000.

Multiple runs. The above procedures generated samples based on 1,000,000 particles (although fewer were stored after the final rejection control). However, even this many samples gave a very imprecise estimate of the posterior distributions of interest for all models. Hence, many multiple runs (100 or more) were required to reduce Monte Carlo error to acceptable levels. To reduce the resulting outputs down to a manageable level for post-processing (i.e., calculating posterior distributions on quantities of interest), it was necessary to apply further rejection control, this time using a rejection control criterion of the 99.999^{th} percentile of the particle weights from all of the multiple runs for a particular model.

One last difference between the algorithm of Thomas and Harwood (2007) and that used here was that the former used an analytic integration procedure to enable efficient estimation of an observation error parameter; here the observation SEs were assumed known.

Estimating total population size

Our state-space model does not include adult males. Nevertheless, if we follow Hammill et al. (2005) and Trzcinski et al. (2006) in assuming male and female survival rates are the same, then total population size can be estimated as twice the adult female population size plus the estimated pup production. We take this approach in giving total population size estimates by region and year, and summed over regions.

RESULTS

Pregnancy rates

The data came from 748 females aged between 2 and 9, of which 509 were found to be pregnant. Plots of age-specific pregnancy rates against time period (1960-70, 1980-90 and 2000-07, Fig. 3) showed no convincing evidence of temporal pattern, although there is a clear increase in pregnancy rate with age. These observations were confirmed by the GAM analysis: a model with age as a smooth function was slightly preferred (using an unbiased risk estimator model selection statistic, Wood 2006) over models including both age and year (Table 2). In addition, the year term was not statistically significant ($p>0.05$) in either the year-only or the age and year models. We therefore did not consider further models where age-specific fecundity changes over time.

We found that a 2-parameter curve of the form

$$p(preg) = \alpha_{\max} \operatorname{logit}^{-1}(\rho(age - 3.5)) \qquad (6)$$

fit the observed age-specific pregnancy rates well (Fig. 4), since it allowed pregnancy rates to be near zero at age 2, and rapidly increase thereafter to be very close to the asymptote by age 6. Nonlinear least squares regression gave estimates of maximum pregnancy rate of α=0.876 (SE 0.015), with rate parameter ρ=2.318 (SE 0.289). Note, when applying these results to the population dynamics model, the ages used in that model are one year greater, since a female that was sampled for the pregnancy rate analysis at age *a* would have given birth at age *a*+1.

State-space model

The results reported here are based on 150 runs of 1 million particles. This represents approximately 150 hours of computer time, although in practice runs were made in parallel on up to 8 processors so results were available in 1-2 days. After the final rejection control step of the particle filtering algorithm, 10.4 million particles remained.

Since the resampling step of the auxiliary particle filter makes multiple copies of the same particles, the surviving particles are no longer independent, so the true sample size of independent particles is much lower than total sample size. A useful approximate index of whether there have been enough runs for Monte-Carlo error to be acceptably low is the total number of unique ancestral particles (i.e., independent samples from the prior) surviving in the final results – for example Thomas and Harwood (2007) aimed to achieve >1000 ancestral particles. The 10.4 million particles contained 11,445 ancestral particles, so we expect Monte-Carlo error to be low. This was confirmed by dividing the particles into two equal halves and checking some inferences on both subsets: for example posterior mean on ϕ_a was 0.967 and 0.969 from the two halves; for $\phi_{p\max}$ the two values were 0.746 and 0.742; for γ the two values were 0.138 and 0.141.

Estimated pup production[1] for the three regions is shown in Fig. 5, and values are given in Appendix Table A3. The estimated trajectory for the Sable region fits the data quite well. The trajectory appears near-exponential, but there is some evidence that the rate of population increase is slowing: mean annual rate of population change was estimated to be 1.12 from 1980-89, 1.11 from 1990-1999 and 1.09 from 2000-2007. The fit to the Gulf region data is rather less impressive, and it is clear that there is something missing from the model to account for the unexplained variation in pup production estimates between closely spaced years. The estimated pup production in 1977 is in the upper part of the prior range, and the estimates show generally decreasing pup production from 1978 through to the late 1980s, corresponding with the higher harvest levels in this period. Pup production has been estimated to be increasing thereafter. The fit to the Eastern Shore data is satisfactory, with the estimated trajectory being one of near exponential increase.

Estimates of total population size at the beginning of each year (i.e., just after the breeding season, and so including pups, but before hunting or natural mortality) are shown by region in Fig. 6 and in Appendix Table A4. The trajectories generally mirror those of the pups. Estimated total population size in 2007, combined over all 3 regions is 304,000 (95% CI 242,000-371,000). This is 6% higher than the equivalent estimate for 2006 of 285,000 (95%CI 230,000-344,000) and 750% higher than the estimate for 1977 of 41,000 (95%CI 31,000-51,000). Estimates of overall mean annual population change were 1.04 from 1980-1989 (depressed due to harvest in the Gulf), 1.09 in 1990-1999, and 1.08 in 2000-2007.

Posterior parameter distributions are shown in Fig. 7, together with the corresponding priors. The fecundity parameters ($\alpha_{\max}$ and ρ) are almost identical to their priors, indicating that effectively nothing has been learnt about these from the pup production data over the information specified in the prior distribution. Posterior maximum juvenile survival ($\phi_{p\max}$) is similar to the prior, although the mean is slightly higher. Posterior mean adult survival (ϕ_a) is also slightly higher (0.97 vs 0.95 in the prior), but the posterior standard error is around a third that of the prior, so the data have somewhat informative about this parameter. The posterior mean on the movement parameter γ is a twentieth that specified by the prior (0.14 vs 2.5), and the standard error is much reduced, implying very little movement of females between regions given the model and data. All three carrying capacity parameters (χ s) have much higher posterior means than priors – for example the prior mean carrying capacity for Sable Island was 100,000 pups (95% CI 27,000-220,000), but the posterior is 417,000 (95% CI 213,000-880,000). Note, however, that the standard errors on the posterior estimates (and hence the CIs) are high – similar to the prior specification of a 50% CV.

[1] Note that all results reported here on states are smoothed rather than filtered estimates, sensu e.g., Cappé 2005. This just means that they are estimates computed using all the data, rather than just the data up to the time point for which the estimate is being made.

DISCUSSION

Reliability of results

There are three reasons why we may wish to interpret the results with caution.

Firstly, the model is clearly inadequate in some respects. It does not explain the large variation between closely-spaced surveys in observed pup production in the Gulf region. We therefore recommend viewing with caution the estimated pup production and total population size coming from this region. We discuss later possible extensions to address this. Our assumption that adult male and female survival is identical is questionable, given that males often have lower survival than females in body-size dimorphic species such as grey seals, as is the assumption that pregnancy rates and fecundity rates are equal among regions.

Secondly, being a Bayesian analysis, it is important to consider the sensitivity of the results to the priors. We anticipate high sensitivity of estimated parameter distributions in parameters where the posterior is very similar to the prior ($\alpha_{\max}$, ρ and $\phi_{p\max}$), and less for the other parameters. This sensitivity may affect the population size estimate somewhat – for example fecundity rate is closely related to population size since the number of breeding females is given by the estimated pup production divided by the fecundity rate. We anticipate that our priors on initial population sizes in 1977 will have little effect on estimates of current population size. These intuitions should, however, be tested. We note that the posterior on carrying capacity for the Eastern Shore region is extremely different from the prior, and this deserves more investigation.

Lastly, the fitting method may have influenced the result, although probably not to any significant extent. We do not think there is much Monte-Carlo error in our results. However, we achieved low MC error in part by trebling the observed SEs on pup production estimates, when evaluating the particle weights. The models should be re-run with the correct SEs – although it will take very significantly more particles to achieve the same reliability in the estimated posterior distributions. Our intuition is that this will have little effect on the posterior means, although it may reduce the SEs a little. We also made an arbitrary assumption to obtain SEs on total counts – although this probably had little effect on the inferences. The particle filtering algorithm included an auxiliary particle filter with kernel smoothing of parameters, and this is known to cause bias in theory, although Newman et al. (in revision) found no discernable difference between PF estimates and those from an MCMC sampler that was used as the "gold standard", with both simulated and real data applied to a seal model similar to the one used here. They used a kernel smoothing discount parameter of 0.997, while we used 0.9997, so we expect even less bias here – although the model and data are different so it is something worth investigating if possible. Attempting very large runs with no kernel smoothing is one possible way to attempt this.

Inferences about grey seal population dynamics

We found that the model used here does not show much evidence of a recent density-dependent slow-down in population growth, when calibrated with the pup production

data. Our posterior estimates of carrying capacity are 6-10 times higher than current estimated levels of pup production; hence if the model is correct then in the absence of changes in management practices, seal populations will continue to rise at similar rates to those seen in the recent past.

There are several reasons why this inference may be incorrect. Some were discussed in the previous section. In addition, carrying capacity is notoriously difficult to estimate from populations still growing rapidly. There is also every reason to expect that changing environmental conditions, or other limitations such as food stocks, may place a limit on seal numbers long before our estimated carrying capacities are reached.

We also found that rather less movement between colonies is required to fit the data than we had anticipated. This is something that bears further investigation.

The analysis of shot adult female seals we performed showed no convincing evidence for a decline in age-specific pregnancy rates. By contrast, data from resightings of branded (marked) animals on Sable Island have shown an increase in mean age at first birth (Bowen et al. 2007). This suggests that density dependent factors may be beginning to operate in this segment of the population, and therefore that different factors may be operating in the different regions. It would be useful to include the Sable Island marked animal data in future analyses of population dynamics.

Future work

There are several directions in which this work could be extended. As mentioned above, the prior sensitivity needs investigating as does any bias caused by the fitting algorithm. There is a clear need to extend the biological model to better match conditions in the Gulf region. Both pre- and post-weaning pup mortality in the Gulf is strongly decreased under a combination of poor ice conditions and storms, and it would be very useful to be able to introduce a covariate to account for this. In addition, it is likely that maximum pup survival is lower in the Gulf than the other regions. Other biological models could be considered, and model selection methods used to evaluate support for each. However, as with British Grey Seals (Thomas and Harwood 2006, 2007), it is likely that there is little information in the data to distinguish between various plausible models. Nevertheless, unlike for British seals, the presence of a time series of information on pregnancy rates means that alternative plausible models are unlikely to predict extremely different total population sizes. Including additional information on survival, particularly adult male survival, would help considerably to improve the reliability of the modelling process.

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Table 1. Prior parameter distributions for the state-space model of grey seal population dynamics.

Param	Distribution	Mean	Stdev
ϕ_a	Be(27.25,1.43)	0.95	0.04
$\phi_{p\max}$	Be(14.00,6.00)	0.7	0.1
χ_1	Ga(4,25000)	100000	50000
χ_2	Ga(4, 7500)	30000	15000
χ_3	Ga(4,1500)	6000	3000
$\alpha_{\max}$	Be(427.50,60.59)	0.876	0.015
ρ	Ga(64.29, 3.61×10^{-2})	2.319	0.29
γ	Ga(1.00,2.5)	2.5	2.5

Table 2. Model selection statistics for Generalized Additive Model analysis of pregnancy rates as a function of seal age and year. s(x) indicates smooth function (a thin plate regression spline with degrees of freedom estimated by the software) of covariate x; s(x,y) indicates a two-dimensional smooth function; f(x) indicates a factor covariate x; and + indicates an additive effect. EDF is estimated degrees of freedom, UBRE score is the unbiased risk estimator model selection score. In general, the model with the smallest UBRE score (highlighted in the table) is preferred (Wood 2006).

Model	EDF	UBRE score
f(age)	8	0.174
s(age)	**4.8**	**0.136**
f(year)	16.0	3.709
s(year)	8.3	3.637
f(age)+s(year)	10.5	0.189
s(age)+s(year)	8.2	0.152
s(age, year)	23.1	0.208

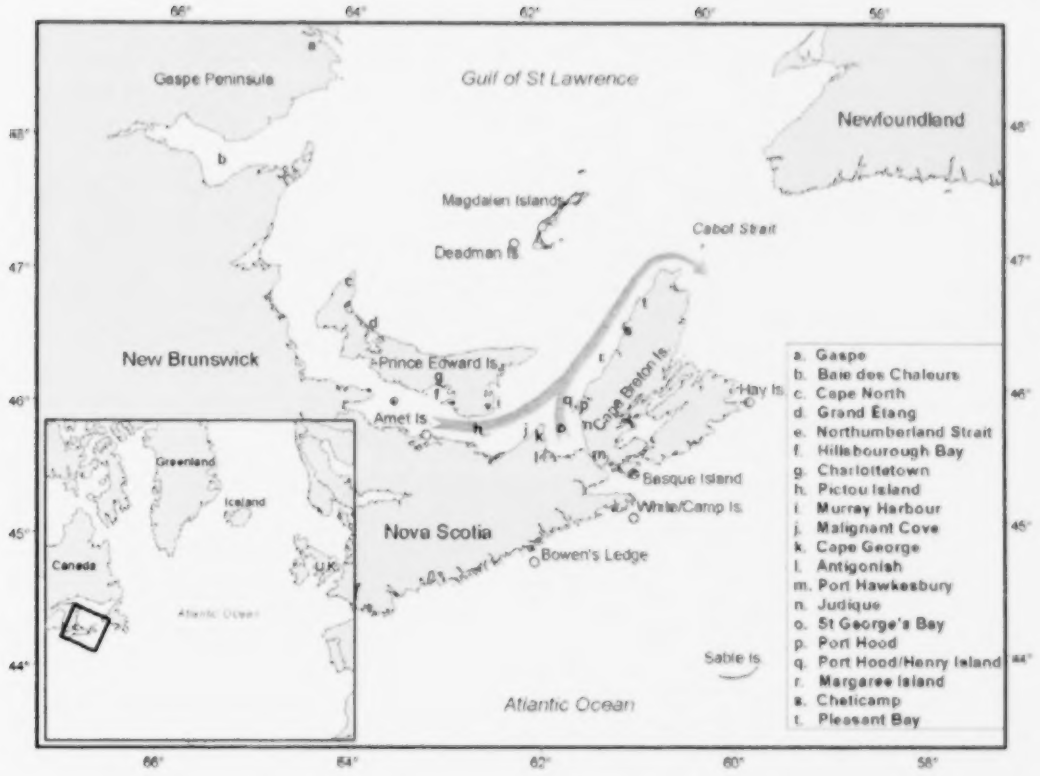

Figure 1. Area of interest in Eastern Canada showing locations where grey seal colonies can be found. The arrow represents the general direction of ice drift for pups born on the pack ice in Northumberland Strait.

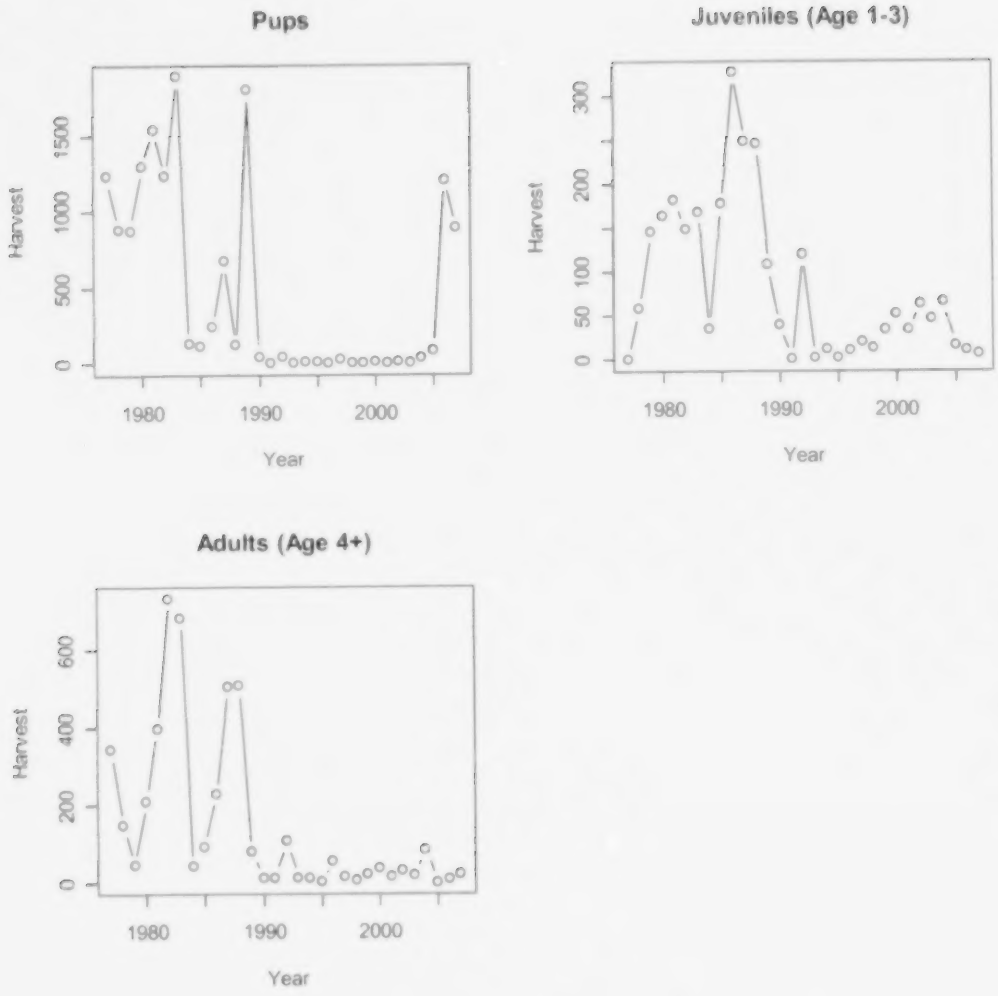

Figure 2. Number of seals harvested by commercial hunt and scientific sampling. Almost are assumed to come from the Gulf region (see Appendix Table A2 for values by region).

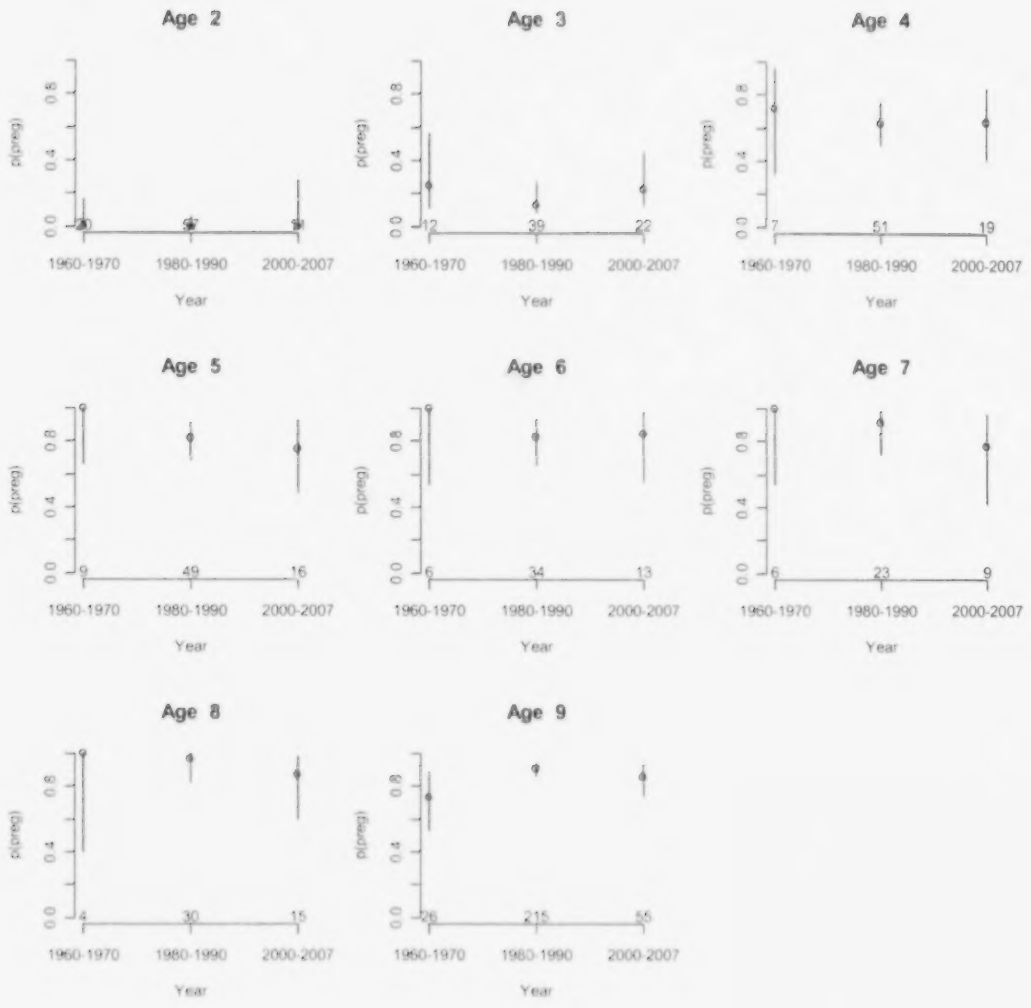

Figure 3. Estimated pregnancy rate by age and time period, with associated 95% binomial confidence intervals. Sample sizes are given below each estimate.

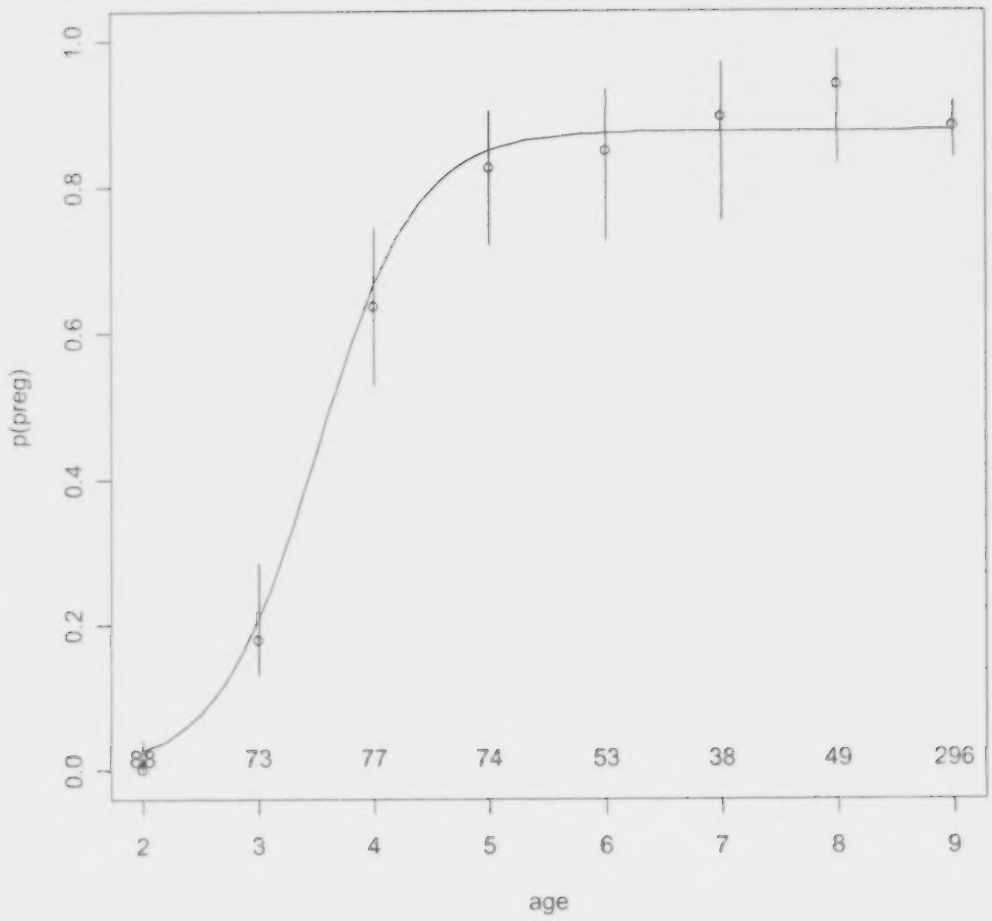

Figure 4. Observed proportion pregnant (p(preg)) at each age class (circles), together with 95% binomial CIs (horizontal lines), and fitted curve of the form $p(preg) = \alpha_{\max} \operatorname{logit}^{-1}(\rho(age - 3.5))$. Sample sizes are given along the bottom.

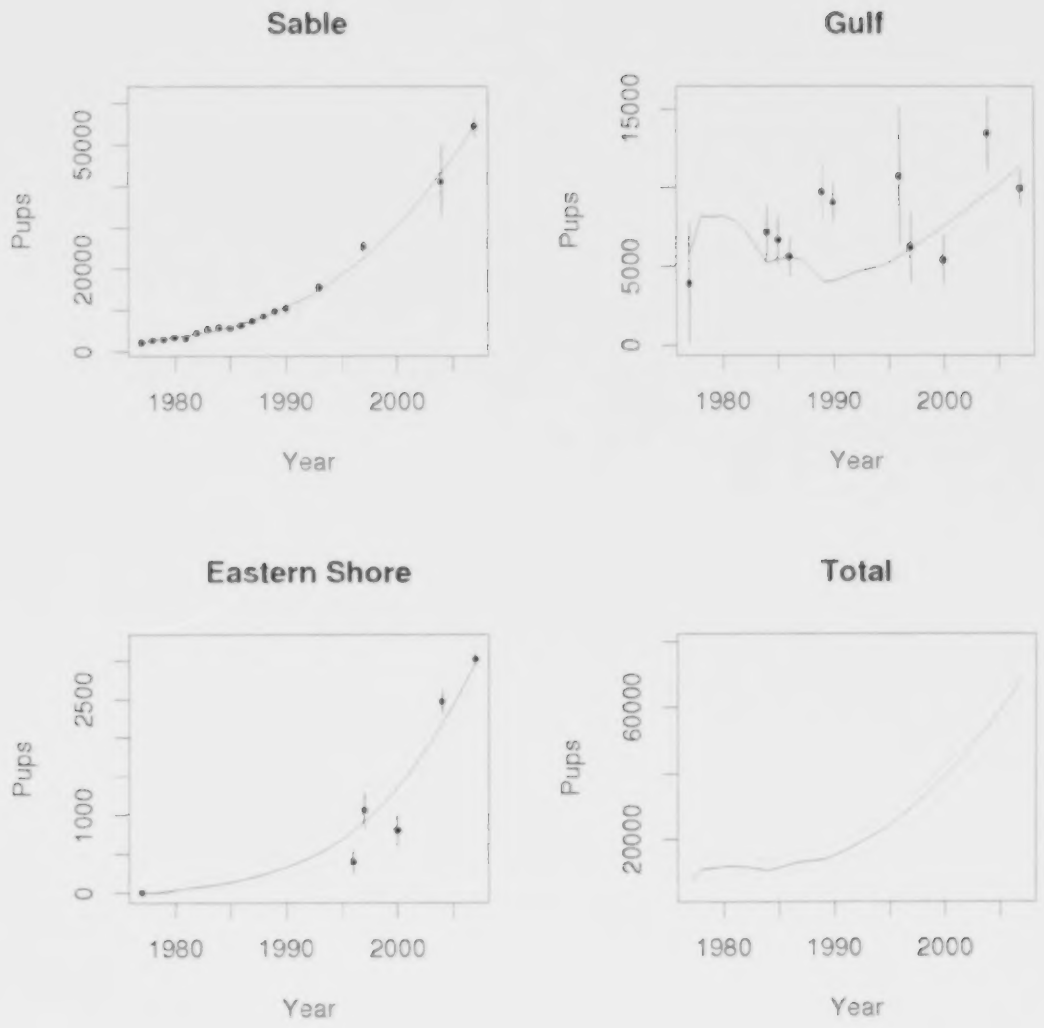

Figure 5. Estimates of true pup production from a model of grey seal population dynamics fit to pup production estimates from 1977-2007 in three regions. The smooth lines show the posterior mean bracketed by the 95% posterior credibility interval. The filled circles show estimated pup production from survey data and the vertical lines denote +/- 2 standard errors on these estimates. Note that the values for Gulf and Eastern Shore in 1977 are not actual data, but used to form the priors on pup production in the first year of the model.

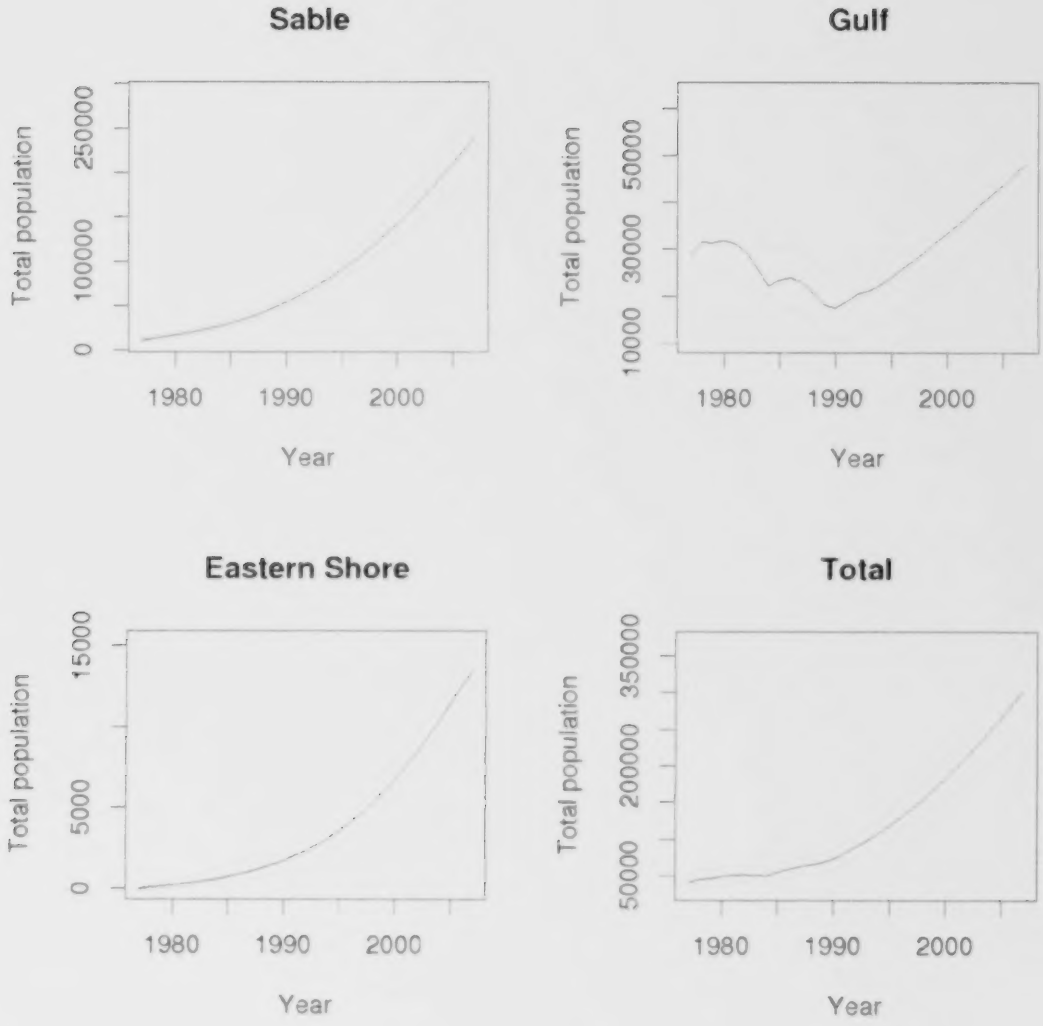

Figure 6. Estimates of total population size (including pups) from a model of grey seal population dynamics fit to pup production estimates from 1977-2007 in three regions. The smooth lines show the posterior mean bracketed by the 95% posterior credibility interval.

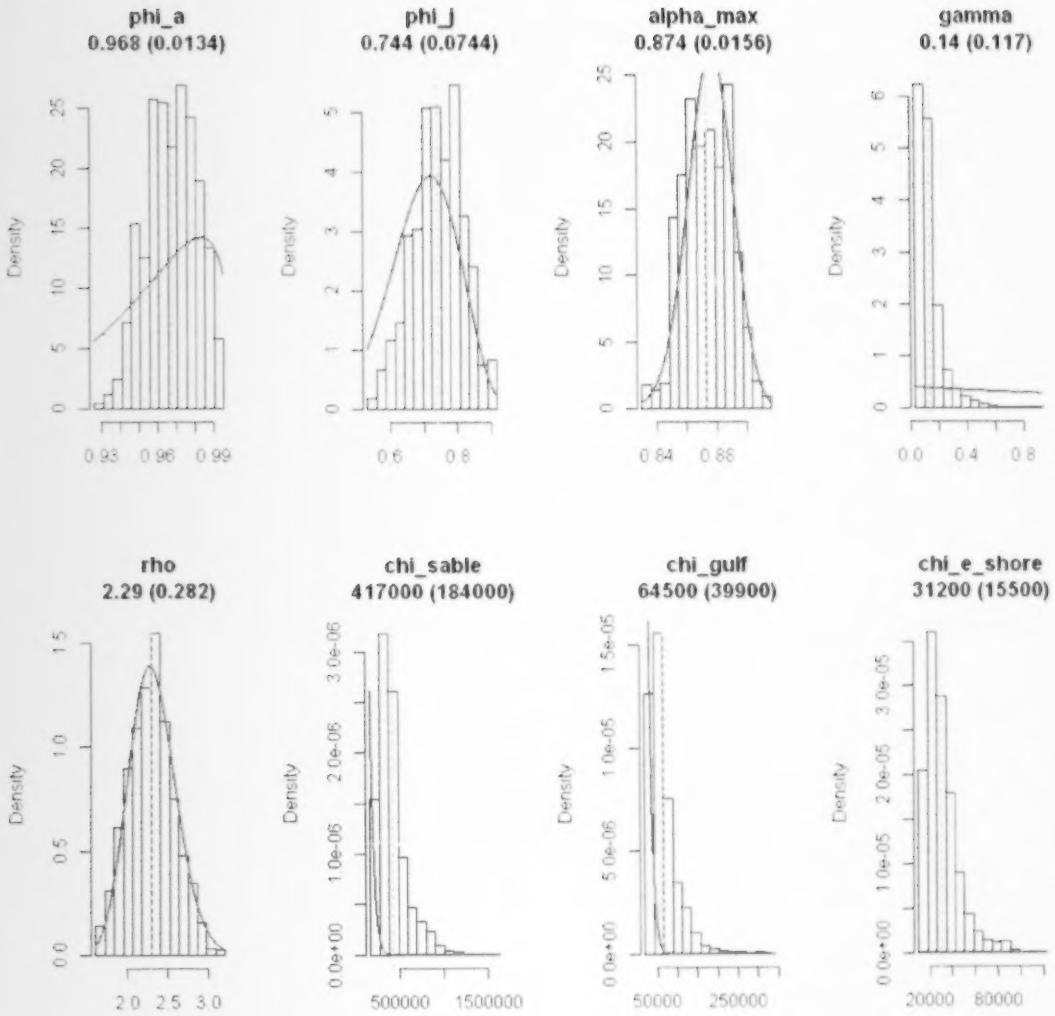

Figure 7. Posterior parameter estimates (histograms) and priors (solid lines) a model of grey seal population dynamics fit to pup production estimates from 1977-2007. The vertical line shows the posterior mean; its value (and standard error) is given in the title of each plot after the parameter name.

Appendix Table A1. Pup production data and associated SEs used in the state-space model analysis. Note that the values for Gulf and Eastern Shore in 1977 (shown in italics) are not actual data, but used to form the priors on pup production in the first year of the model.

Year	Sable Island		Gulf		Eastern Shore	
	Estimate	SE	Estimate	SE	Estimate	SE
1977	2181	173	*3900*	*950*	*0*	*0*
1978	2687	192				
1979	2933	201				
1980	3344	214				
1981	3143	208				
1982	4489	248				
1983	5435	273				
1984	5856	283	7151	907		
1985	5606	277	6668	784		
1986	6301	294	5607	654		
1987	7391	318				
1988	8593	343				
1989	9712	365	9710	901		
1990	10451	575	9049	639		
1991						
1992						
1993	15500	463				
1994						
1995						
1996			10715	2240	395	74
1997	25400	750	6229	1190	1061	121
1998						
1999						
2000			5389	810	799	105
2001						
2002						
2003						
2004	41100	4381	13431	1200	2469	76
2005						
2006						
2007	54482	1288	9948	594	3017	40

Appendix Table A2. Harvest data used in the state-space model analysis. Age and region categories not shown are all zero.

Year	Sable Island	Gulf			Eastern Shore	
	Adults	Pups	Juveniles	Adults	Pups	Adults
1977	0	1229	0	342	0	0
1978	0	882	58	147	0	0
1979	0	875	146	45	0	0
1980	0	1298	164	211	0	0
1981	0	1535	182	397	0	0
1982	0	1230	149	731	0	0
1983	108	1886	168	682	0	0
1984	16	128	35	41	0	0
1985	0	113	177	91	0	0
1986	0	242	327	228	0	0
1987	0	672	248	505	0	0
1988	0	121	246	506	0	0
1989	0	1799	108	79	0	0
1990	0	38	39	13	0	0
1991	0	0	0	13	0	0
1992	0	44	119	106	0	0
1993	0	0	1	12	0	0
1994	0	7	11	11	0	0
1995	0	7	2	1	0	0
1996	0	4	10	55	0	0
1997	0	23	19	14	0	0
1998	0	1	13	6	0	0
1999	0	2	34	20	0	0
2000	0	9	51	37	0	0
2001	0	2	33	15	0	0
2002	0	8	63	31	0	0
2003	0	2	46	18	0	0
2004	0	31	65	82	0	0
2005	0	85	15	0	494	0
2006	0	1200	10	9	830	0
2007	0	887	6	20	0	91

Appendix Table A3. Posterior estimates of pup production with 95% symmetric Bayesian Credibility Intervals (CIs).

Year	Sable Island	Gulf	Eastern Shore	Total
1977	2 (1.5 2.7)	5.7 (2.7 9)	0 (0 0)	7.7 (4.2 11.6)
1978	2.7 (2.3 3.2)	8.2 (5.4 11)	0 (0 0)	10.9 (7.7 14.2)
1979	3.1 (2.6 3.6)	8.1 (5.6 10.9)	0 (0 0)	11.2 (8.2 14.4)
1980	3.4 (3 3.9)	8.2 (5.9 11)	0 (0 0.1)	11.7 (8.9 15)
1981	3.8 (3.4 4.3)	7.9 (5.8 10.7)	0.1 (0 0.1)	11.8 (9.2 15.1)
1982	4.2 (3.8 4.8)	7.3 (5.3 10)	0.1 (0 0.2)	11.6 (9.1 14.9)
1983	4.8 (4.3 5.3)	6.2 (4.3 8.7)	0.1 (0 0.2)	11 (8.7 14.2)
1984	5.2 (4.7 5.8)	5.2 (3.4 7.6)	0.1 (0 0.2)	10.6 (8.2 13.6)
1985	5.9 (5.3 6.5)	5.4 (3.6 7.6)	0.1 (0.1 0.3)	11.5 (9 14.4)
1986	6.7 (6.1 7.4)	5.6 (3.8 7.6)	0.2 (0.1 0.3)	12.5 (10 15.3)
1987	7.6 (6.9 8.3)	5.4 (3.6 7.4)	0.2 (0.1 0.4)	13.2 (10.7 16.1)
1988	8.6 (7.8 9.4)	4.7 (2.9 6.7)	0.2 (0.1 0.4)	13.5 (10.8 16.5)
1989	9.6 (8.8 10.5)	4 (2.2 5.9)	0.3 (0.2 0.5)	13.9 (11.1 16.9)
1990	10.8 (9.8 11.8)	4.1 (2.2 5.9)	0.3 (0.2 0.5)	15.2 (12.2 18.3)
1991	12.1 (11 13.2)	4.3 (2.4 6.1)	0.4 (0.2 0.6)	16.8 (13.6 19.9)
1992	13.5 (12.2 14.8)	4.6 (2.7 6.4)	0.4 (0.3 0.7)	18.6 (15.2 21.9)
1993	15 (13.6 16.6)	4.8 (2.8 6.6)	0.5 (0.4 0.8)	20.3 (16.8 24)
1994	16.8 (15.1 18.5)	4.9 (2.9 6.9)	0.6 (0.4 0.9)	22.3 (18.4 26.2)
1995	18.6 (16.8 20.6)	5.2 (3.2 7.2)	0.7 (0.5 1)	24.5 (20.4 28.7)
1996	20.7 (18.6 22.8)	5.7 (3.6 7.6)	0.8 (0.6 1.1)	27.1 (22.8 31.5)
1997	22.9 (20.6 25.3)	6.1 (4 8.1)	0.9 (0.7 1.2)	29.8 (25.2 34.5)
1998	25.2 (22.7 27.9)	6.6 (4.4 8.6)	1.1 (0.8 1.4)	32.8 (27.9 37.8)
1999	27.8 (25 30.7)	7.1 (4.9 9.1)	1.2 (1 1.5)	36.1 (30.8 41.4)
2000	30.5 (27.4 33.8)	7.6 (5.4 9.7)	1.4 (1.1 1.7)	39.4 (33.9 45.1)
2001	33.4 (30.1 37)	8.1 (5.8 10.3)	1.5 (1.3 1.8)	43 (37.2 49.1)
2002	36.5 (32.8 40.5)	8.6 (6.3 10.9)	1.7 (1.5 2)	46.8 (40.6 53.4)
2003	39.8 (35.6 44.3)	9.1 (6.8 11.5)	2 (1.7 2.2)	50.9 (44.1 58)
2004	43.2 (38.5 48.3)	9.7 (7.2 12.2)	2.2 (2 2.4)	55.1 (47.7 62.9)
2005	46.9 (41.5 52.5)	10.2 (7.6 12.8)	2.4 (2.2 2.7)	59.5 (51.4 68)
2006	50.6 (44.5 57)	10.8 (8.1 13.6)	2.7 (2.5 2.9)	64.1 (55 73.5)
2007	54.6 (47.5 61.8)	11.4 (8.4 14.4)	3 (2.8 3.2)	69 (58.7 79.4)

Appendix Table A4. Posterior estimates of total population size at the end of each breeding season (i.e., including pups), with 95% symmetric Bayesian Credibility Intervals (CIs).

Year	Sable Island	Gulf	Eastern Shore	Total
1977	11.9 (10.2 14.3)	28.7 (20.6 37)	0 (0 0)	40.6 (30.8 51.2)
1978	13.6 (11.5 16.3)	31.4 (23.6 39.9)	0.1 (0 0.2)	45.2 (35.2 56.4)
1979	15.4 (13 18.2)	31.4 (23.8 39.5)	0.1 (0.1 0.3)	47 (36.9 58)
1980	17.5 (15 20.4)	31.8 (24.9 39.6)	0.2 (0.1 0.5)	49.5 (39.9 60.5)
1981	19.7 (17.1 23.1)	31.2 (24.3 38.5)	0.3 (0.1 0.7)	51.2 (41.5 62.3)
1982	22.2 (19.5 25.7)	29.4 (22.6 36.5)	0.4 (0.1 0.8)	52 (42.2 63.1)
1983	25.1 (22.1 28.7)	26 (19.3 32.8)	0.5 (0.2 1)	51.5 (41.5 62.5)
1984	27.6 (24.3 31.5)	22.2 (15 29.2)	0.6 (0.3 1.2)	50.4 (39.6 61.9)
1985	31 (27.4 35.1)	23.4 (16.4 30.2)	0.8 (0.4 1.4)	55.1 (44.1 66.7)
1986	34.8 (31 39.4)	23.9 (17.1 30.4)	0.9 (0.5 1.7)	59.6 (48.6 71.4)
1987	39 (34.8 43.9)	23 (16.2 29.4)	1.1 (0.6 1.9)	63.1 (51.6 75.2)
1988	43.7 (39.1 48.7)	20.5 (13.5 27)	1.3 (0.8 2.2)	65.5 (53.3 77.9)
1989	48.9 (43.7 54.1)	18.1 (11 24.9)	1.5 (0.9 2.5)	68.6 (55.6 81.5)
1990	54.5 (48.7 60.2)	17.4 (10.2 24.7)	1.7 (1.1 2.8)	73.6 (60 87.7)
1991	60.6 (54.4 67.1)	18.8 (11.2 26)	2 (1.3 3.1)	81.5 (67 96.2)
1992	67.4 (60.5 74.5)	20.4 (12.7 27.7)	2.3 (1.6 3.5)	90.1 (74.8 105.7)
1993	74.7 (67.1 82.7)	21 (13.1 28.4)	2.7 (1.9 3.9)	98.4 (82.1 115)
1994	82.6 (74.1 91.6)	22.5 (14.4 30.1)	3.1 (2.2 4.4)	108.2 (90.7 126)
1995	91.1 (81.6 101.1)	24.1 (15.8 31.9)	3.6 (2.7 4.8)	118.8 (100.1 137.9)
1996	100.3 (89.6 111.7)	25.9 (17.4 34)	4.1 (3.1 5.4)	130.4 (110.1 151.1)
1997	110.1 (98.2 123.1)	27.5 (18.9 35.9)	4.7 (3.7 6)	142.3 (120.8 164.9)
1998	120.6 (107 135.3)	29.5 (20.9 38.1)	5.3 (4.3 6.6)	155.4 (132.3 180)
1999	131.7 (116.3 148.3)	31.5 (22.8 40.5)	6 (5 7.2)	169.2 (144.1 196)
2000	143.5 (125.8 162.3)	33.4 (24.5 42.7)	6.8 (5.8 8)	183.6 (156 213)
2001	155.9 (135.4 177.1)	35.4 (26.2 45.2)	7.6 (6.6 8.8)	198.8 (168.2 231)
2002	168.9 (145.2 193.1)	37.5 (27.9 47.9)	8.5 (7.5 9.6)	214.9 (180.6 250.5)
2003	182.5 (155.1 210.3)	39.6 (29.6 50.6)	9.4 (8.5 10.6)	231.6 (193.2 271.5)
2004	196.8 (165.2 228.9)	41.7 (31 53.5)	10.4 (9.4 11.7)	248.9 (205.5 294.1)
2005	211.5 (175.4 248.7)	43.7 (32.2 56.6)	11.5 (10.2 12.9)	266.7 (217.8 318.2)
2006	226.8 (185.6 269.6)	46.1 (33.6 60.2)	12.6 (11 14.2)	285.4 (230.3 344)
2007	242.2 (195.8 291.6)	48.2 (34.7 63.5)	13.5 (11.9 15.4)	303.9 (242.4 370.5)